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# 7 Rodent seed hoarding and regeneration of *Aesculus turbinata*: patterns, processes and implications

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## 7.1 Introduction

Tree regeneration is often limited by seed abundance, herbivore activities, and microhabitat suitability (Crawley 2000). In montaneous riparian habitats, tree seedling establishment often depends on particular microhabitats associated with the disturbance regime (e.g. gravel debris and mineral soil exposure; Sakio 1997; Kubo et al. 2000; Masaki et al. 2007). However, the Japanese horsechestnut, *Aesculus turbinata* Blume (Hippocastanaceae), is a tree species that is common in montane riparian forests but does not appear to have particular requirements for establishment. The reproductive traits of this species are characterized by conspicuously large inflorescences and extremely large seeds (21g in fresh weight and 6.2 g in dry weight). In general, large seeds provide a greater chance of seedling establishment through persistence under shade and resistance to disease (Westoby et al. 1992).

In riparian heterogeneous environments, seed dispersal may play important roles in enhancing the success of regeneration. Considering the large amounts of seed reserves, seedlings of large-seeded trees would be to some extent tolerant of physical conditions in particular environments such as germination substrates, and water and nutrient availability (Westoby et al. 1992). Therefore, regeneration success may depend on how wide the seeds are dispersed, to e.g. various topographic units and patches separated by fluvial disturbances. Actually, large seeds of *Juglans ailanthifolia* Carr., also dispersed by rodents and squirrels, are often delivered to floodplains isolated by channels irrespective of microtopography, and contribute to riparian dominance for the species (Goto & Hayashida 2002).

The regeneration of large-seeded species is often affected by small mammals (Crawley 2000), especially rodents which are often responsible for the regener-

ation, in opposite ways. First, since large seeds and seedlings are attractive foods for herbivores, rodents may act as antagonistic seed/seedling predators (Janzen 1971; Hulme 1993; Crawley & Long 1995). On the other hand, rodents rigorously collect, transport and hoard more seeds than they immediately consume (caching behavior); they can also be mutualistic seed dispersers (Vander Wall 1990, 2001). Although a number of studies have examined the ecological role of seed dispersal (e.g. Nakashizuka et al. 1995), little attention has been paid to when and how those seeds die through rodent seed-hoarding processes and its consequences for the plants (Vander Wall & Joyner 1998; Hoshizaki & Hulme 2002).

In this chapter, I review studies on the regeneration of *A. turbinata* (Hoshizaki et al. 1997, 1999; Hoshizaki & Hulme 2002). Emphasis is placed primarily on its seed and seedling demography. First, I describe patterns and processes of seed hoarding by rodents. In the second part, the seedling ecology of *A. turbinata* is reviewed. Finally, the ecological significance of seed hoarding for *A. turbinata* is explained. I also discuss whether the relationship among *A. turbinata* and rodents is mutualistic or antagonistic. Implications of rodent-mediated regeneration in riparian habitat structures and for life history are presented.

## 7.2 Methods

### 7.2.1 Study forest

The studies were undertaken in the Kanumazawa Riparian Research Forest (4.71 ha). The forest contains ca. 2.8 ha of undisturbed riparian area consisting of a diverse array of tree species (Suzuki et al. 2002; Masaki et al. this volume). *A. turbinata* is one of the dominant tree species in the riparian area, comprising 18.5% of total basal area (Suzuki et al. 2002). A 0.4-ha plot (50 × 80 m) and a 1-ha plot (100 × 100 m) were used in the forest. The former was established to track the fate of *A. turbinata* seeds removed by rodents, and 5 of 8 adult (i.e. reproductive) trees were investigated (Hoshizaki et al. 1999). In the 1-ha plot, seedfall and seedling censuses of major tree species has been investigated extensively for years (Hoshizaki et al. 1997; Masaki et al. 2007). Twenty adults of *A. turbinata* are included.

### 7.2.2 Seed tracking and final destinations

Among several methods used to track rodent-dispersed seeds, thread- or wire-tagging is the simplest way and can be applied most effectively to relatively large seeds. It is advantageous in that tagged seeds can be tracked longer: from seedfall until seedling emergence. By installing seeds tagged with a 40-cm-long wire during 1995-1997 in the 0.4-ha plot, the complete fate of 337 seeds of *A. turbinata* that had fallen from the 5 adults selected as source trees was followed (Hoshizaki & Hulme 2002).

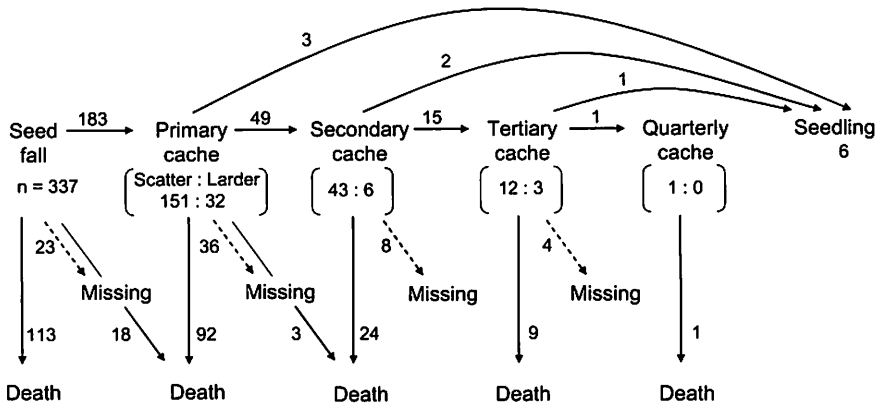


Fig. 1. Seed fate pathways for *Aesculus turbinata*. Numbers along each arrow indicate the seed numbers pooled for 1995-1997. Data reanalyzed from Hoshizaki & Hulme (2002)

The final destination of a seed is the site of seedling emergence. Since *A. turbinata* shows hypogeal germination, the seed coat remains attached to the emerging seedling (Hoshizaki & Miguchi 2005). Using this characteristic feature, the destination of fallen seeds of *A. turbinata* was investigated (Hoshizaki et al. 1999). A total of 1731 seeds were marked with ink on the seed coat and placed under 5 source trees in the 0.4-ha plot. During the season of seedling emergence, the hypogeal cotyledons of all the emerging seedlings were checked.

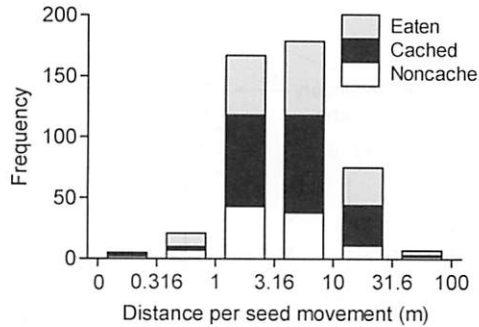
### 7.2.3 Spatial pattern of seedfall and seedling census

Seedfall was monitored using 121 seed traps with 10-m regular spacing in the 1-ha plot. Emerged seedlings were sampled throughout the plot, and their locations recorded (Hoshizaki et al. 1997). Survival was checked at least once a month, with any herbivore damages recorded.

## 7.3 Seed dynamics: cache generation, retrieval and consumption

### 7.3.1 How often are the seeds hoarded?

In research on seed dispersal by seed-hoarding animals, a primitive question is how often the seeds are removed, hoarded, and consumed (Forget 1990; Isaji & Sugita 1997). Rodents removed 95.8% of the seeds marked (n = 337 in total). They removed only intact seeds. Those infested by insects were not taken. Among the seeds removed, 183 (56.7%) were cached (primary cache; Fig. 1), which is



**Fig. 2.** Frequency distribution of seed transportation distances by rodents. Note that distance classes were categorized on a log scale, by every seed status: eaten, newly cached, or only transported (noncache)



**Fig. 3.** *Apodemus speciosus* having an *Aesculus turbinata* seed in its mouth. The mouse is just entering a 'camera trap' from above. Scales indicate 1 cm for dots and 5 cm for black lines. Photo taken with a far-infrared sensor, by K. Hoshizaki

1.85-times the number consumed immediately after removal (99 seeds). Primary caches were placed mostly within 10-20 days (depending on year) after the seed-fall.

Caches experienced several rounds of retrieval and recaching. Each seed was handled by rodents on average  $2.2 \pm 1.2$  times after seedfall until its ultimate fate (death or seedling emergence). Forty nine seeds experienced secondary caches, 15 experienced tertiary caches, and one experienced quarterly cache (Fig. 1). Seeds were sometimes left on the forest floor ('noncache' status) after being transported.

Rodents handled seeds at relatively short intervals; a handling interval of 2 days was most frequent, and 75.7% of all seed handlings occurred within 8 days.

### 7.3.2 Seed transportation and the dispersal agent

A rodent carries a single *A. turbinata* seed in its mouth when transporting it (Fig. 3). Camera-trapping revealed that the large Japanese field mouse *Apodemus speciosus* is the legitimate seed disperser (Hoshizaki 1999). At each carry, these rodents moved seeds a wide range of distances, from only 10 cm to 50.4 m. In most cases, the distance moved ranged from 1 to 10 m (Fig. 2). There seemed no difference in distances moved among cache status (eaten, newly cached, or noncache) in these dominant classes. In contrast, rodents tended to cache seeds after transporting them as far as 30 m or more, but this comparison seems premature because sample sizes are small.

### 7.3.3 Scatter- vs. larder-hoarding

Rodents placed mostly scatterhoard over larderhoard caches. Larderhoard caches occupied only 17.4% (n=32) of the primary caches, 12.2% of the secondary caches, and 20.0% of the tertiary caches. In 1996, when rodent density was highest among the three years studied, primary caches included more larder hoards (52.5%) than in the other two years (7.7%, average of 1995 and 1997). The fate of larderhoarded seeds was death in all cases. These results suggest that when the density of seed hoarders is high, rodents become more eager to quickly acquire their own food, free from cache pilferage, than to store foods for later use (Vander Wall & Joyner 1998).

Scatterhoard caches usually contained a single seed, with from 1 to 3 seeds per cache (Hoshizaki & Hulme 2002). All the seedlings from the marked seeds emerged from scatterhoard caches. Nevertheless, seedlings were sometimes found in large clumps of >10 individuals (see below), indicating that larger caches can eventually emerge. Thus, rodents typically transport the seeds several times from cache site to cache site. These relocations would benefit single-seeded caches to increase the distance between caches, probably contributing to a spatially even distribution of seedlings (see below).

## 7.4 End-points of seed dispersal

### 7.4.1 Dispersal distance

How far can rodents move seeds away from the source tree? As mentioned above, seed dispersal distance can be directly measured by tracking seeds at the time of seedling emergence whose seed coat was marked after seedfall. The result

revealed that the seeds had been moved considerable distances during autumn and winter. The seeds were sometimes moved beyond the crown projection of neighboring fruiting trees. The frequency distribution of seed dispersal distances showed that the tail of the seed shadow reaches up to 115 m from the source tree (12.2-44.7 m for means,  $n = 2$  years; Fig. 4). This is comparable to or greater than other large seeds, *Quercus* spp. and *Fagus crenata* (Jensen & Nielsen 1986; Miguchi 1994; Iida 1996).

Seed dispersal events where the distance from source trees is  $>100$  m indicate that long-distance dispersal (LDD) can occur via seed hoarding by rodents. The seed dispersal curves of *A. turbinata* suggest that LDD is a relatively minor event in this species, and any unusual behavior in rodents can cause LDD (Higgins et al. 2003). However, LDD might play an important role in establishing a new habitat after perturbations and in the historical spread of populations after climate change (e.g. post-glacial spread; Clark et al. 1998).

#### 7.4.2 Spatial patterns of seedfall and seedling emergence

The distribution of seedlings that emerged (i.e. seedling shadows) in the 1-ha plot was quite different from the seed shadows. In the case of a seedling cohort in 1993, prior seedfalls concentrated (87 %) under the crowns of *A. turbinata*, whereas few seeds fell under other species and in gaps. Despite that, more seedlings emerged in gaps and under the canopy of other species than expected from seedfall densities (Figs. 5, 6a). This tendency was consistent for most cohorts (Hoshizaki et al. 1997).

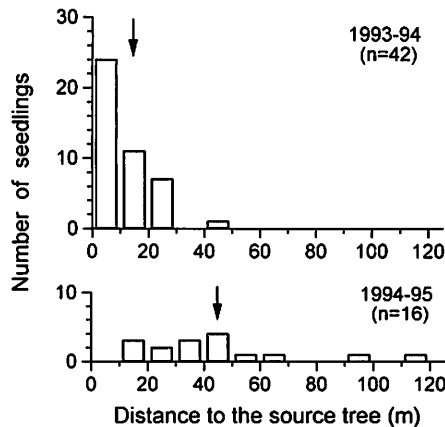
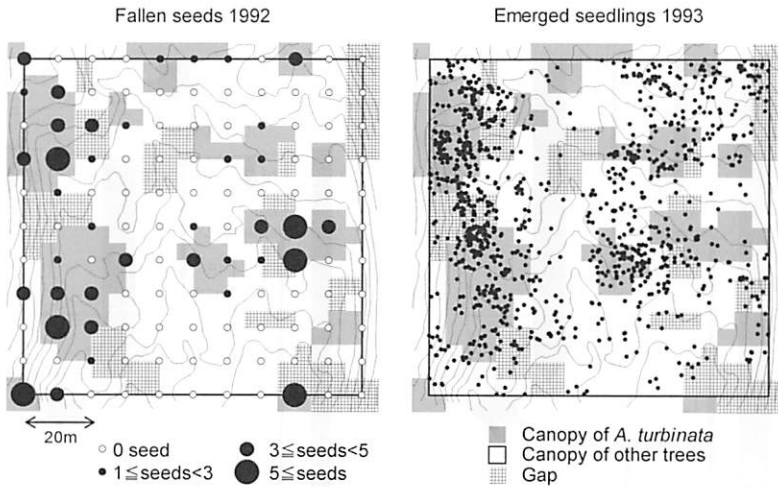
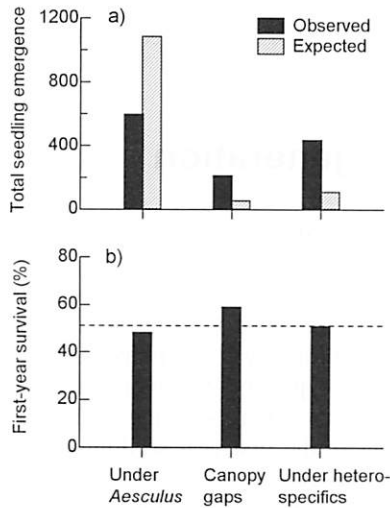


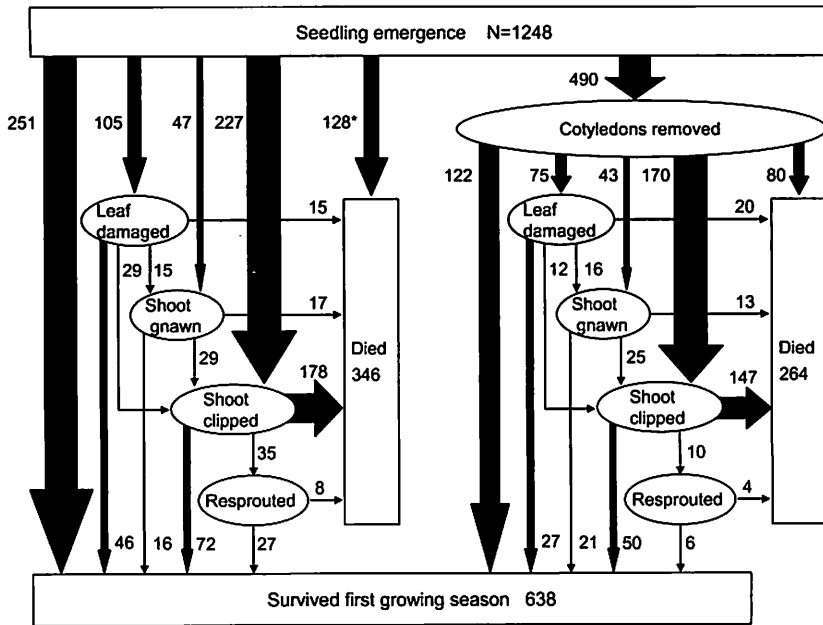
Fig. 4. Seed dispersal curves in *A. turbinata*. Data for seedlings whose source trees were identified by seed-marking in 1993 (upper) and 1994 (lower). The arrow indicates mean dispersal distance for each year (12.2 m for 1993-94 and 44.7 m for 1994-95). After Hoshizaki et al. (1999).



**Fig. 5.** Seedling spatial distribution in a “successful dispersal” year, after enlargement of seed shadows via rodent hoarding activities. Note that seedfall concentrates beneath *A. turbinata* canopies (left) but that seedlings in the following spring emerged over the 1-ha plot (right). Modified from Hoshizaki et al. (1997), with permission



**Fig. 6.** A test of the colonization hypothesis for the adaptive significance of seed dispersal in *A. turbinata*. Expected values, calculated under the assumption that (a) emergence and (b) survival of seedlings are, respectively, proportional to seedfalls and emergence, are shown with (a) hatched bars and (b) the broken line. Data from Hoshizaki et al. (1997)



**Fig. 7.** Fate pathways of first-year seedlings. Numerals represent the number of seedlings for each transition. Width of arrows indicates the importance of each transition. The transition with an asterisked number represents deaths due to only pathogenic fungi and/or light shortage (see also text). Redrawn from Hoshizaki et al. (1997), with permission.

## 7.5 Seedling regeneration

### 7.5.1 Impacts of herbivory

What kinds of hazards are there during the first year of seedling emergence, and how does a large seed mass influence seedling survival? A detailed observation of the fate of current-year seedlings was continued for 4 years (1993-1997). Seedlings experienced various types of herbivory including shoot clipping and cotyledon removal by rodents. Many seedlings suffered from different types of herbivory. Therefore fates of the first-year seedlings had complex pathways (Fig. 7). In the case of a large cohort that emerged in 1993 (1248 seedlings/ha), 39% of seedlings suffered cotyledon removal ( $n = 490$ ), almost the same fraction experienced shoot clipping ( $n = 492$ ), and 207 experienced both types of herbivory.

Shoot clipping had the largest effect on seedling mortality, followed by cotyledon removal (Hoshizaki et al. 1997). In contrast, leaf herbivory rarely resulted in death. Although the detection of mortality factors is difficult, 58% of the seedlings suffering rodent herbivory ultimately died ( $n = 467$ ). This represents

77% of all deaths (Fig. 7). On the other hand, the mortality of intact seedlings, mostly caused by pathogenic fungi, was lower (34%) and accounted only for 21% of total deaths. These results indicate the importance of rodent herbivory and high tolerance to shade and/or pathogens during the first growing season (Hoshizaki et al. 1997).

### 7.5.2 Seedling resistance and the roles of a large seed mass

Seedlings show high resistance to herbivory. In the case of the above cohort, there was no herbivory type that caused 100% mortality, and 32% (n=155) of clipped seedlings survived. The large seed reserves probably contributed to the enhanced tolerance. Furthermore, in *A. turbinata*, because remaining seed reserves are still rich in hypogeal cotyledons even one month after emergence, some seedlings were able to re-sprout after the shoot was clipped. Stored reserves in the hypogeal cotyledons play a pivotal role in resprouting (Hoshizaki et al. 1997; Hoshizaki & Miguchi 2005). The large seed mass of *A. turbinata* thus serves a risk spreading against herbivory (Forget 1992; Harms & Dalling 1997).

Another role of the large seed mass of *A. turbinata* may lie in becoming tall in the riparian understory. It has been suggested that strong pressure of competition with neighboring plants for light on the forest floor can favor a large seed mass (Westoby et al. 1992). Growth of the first year seedling of *A. turbinata* is characteristic in that it quickly reaches ca. 40 cm tall and expands all leaves within 2-3 wk after emergence, but its shoot does not elongate further until the second year (Seiwa & Kikuzawa 1991; Hoshizaki & Miguchi 2005). The seedlings show higher biomass allocation to aboveground parts (3.9-fold larger than to roots), which is much higher than in other large-seeded trees, *Q. crispula* and *F. crenata* (by a factor of 1.8 and 0.53, respectively). Because the understory of riparian forests often has a dense cover of herbaceous/fern species (Hoshizaki & Akiyoshi, unpublished), this distinct feature of seedling morphology may suggest that *A. turbinata* seedlings are competitive in riparian forest floor environments.

Thus the large seed size of *A. turbinata* plays important roles in resistance to damage from herbivores and competition with other plants in the dense understory during the seedling stage.

### 7.5.3 Influence of canopy gaps and density

Canopy gaps provide increased light levels, making them the most crucial microhabitat for regeneration in many species (e.g. Nakashizuka 1983; Schupp et al. 1989). In *A. turbinata*, seedlings survived significantly well in gaps (Fig. 6b, Hoshizaki et al. 1997). Saplings also showed higher growth rates in sites with higher light levels (Hoshizaki et al. 1999). The frequency of herbivory did not differ among canopy conditions, irrespective of the type of damage (Hoshizaki et al. 1997). Other microhabitats (microtopography, rooting substrate, etc.) did not affect seedling survival for *A. turbinata* (Hoshizaki et al. unpublished).

Seedling survival is often negatively affected by density, and this has been emphasized for demography and population dynamics (e.g. Augspurger & Kitajima 1992) and for species richness of forest communities (Janzen 1970). In *A. turbinata*, seedling survival was affected by the local density at emergence; when the density was low enough (1 seedling per 25 m<sup>2</sup>), the survival rate was significantly increased. The causal factor was not obvious, however. Mortality from fungal attacks increased at higher seedling densities, but those from herbivory, the most important factor (Sect. 5.1), did not vary as a function of density (Hoshizaki et al. 1997).

Thus regeneration of *A. turbinata* is strongly limited by herbivores (sensu Crawley 2000) and enhanced in canopy gaps. The little effect of microsites and seed abundance (see below) indicates an advantage of the large seed size of this species.

## 7.6 Ecological roles of seed dispersal by rodents

### 7.6.1 Testing hypotheses regarding adaptive significance

One may expect that seed dispersal involves a selective advantage when dispersed offspring show enhanced performance compared to non-dispersed offspring (Willson 1992; Nakashizuka et al. 1995). Three hypotheses have been proposed regarding adaptive significance: colonization, escape, and directed dispersal (Howe & Smallwood 1982; Willson 1992). To date, comprehensive tests for small mammal-dispersed plants have been scarce, compared to other dispersal systems (Hanzawa et al. 1988; Augspurger & Kitajima 1992; Jordano & Schupp 2000). Moreover, there has been a bias toward the colonization and escape hypotheses in earlier studies (e.g. Janzen 1970, 1971; Schupp et al. 1989; but see Nakashizuka et al. 1995). In *A. turbinata*, all three hypotheses have been tested (Hoshizaki et al. 1997, 1999).

The simplest way of testing was shown for the colonization hypothesis. As mentioned above, the seedlings showed higher performance in canopy gaps, suggesting that gaps are suitable sites for successful regeneration in *A. turbinata*. Second, densities of seedling emergence were similar between in canopy gaps and beneath the canopy of other species (Fig. 6a). Therefore the colonization hypothesis was supported (Hoshizaki et al. 1997). The dispersal distance curve (Fig. 4) suggests that seeds of *A. turbinata* have the capability of reaching canopy gaps.

In the escape hypothesis, detection of positive density-dependent mortality should be a prerequisite for the test, but the causes of the density dependence should also be specified to interpret the plant-enemy interactions (Janzen 1970, 1971). A substantial amount of evidence has been found in support of this hypothesis (e.g. Augspurger & Kitajima 1992; Peres et al. 1997). In *A. turbinata* seedlings, the density dependence of mortality from fungal attacks suggests

support for this hypothesis. However, because this mortality was a minor hazard, as mentioned above, the importance of this hypothesis seems weak (Hoshizaki et al. 1999).

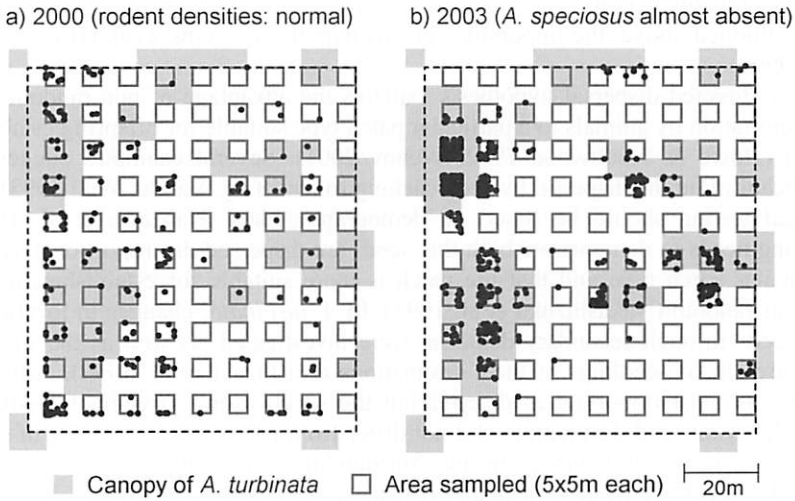
The directed dispersal hypothesis explains the advantage of non-random seed transportation by animals to a particular patch type suitable for offspring establishment (Howe & Smallwood 1982; Wenny 2001). Several examples suggest its applicability to the dispersal by seed-caching rodents (e.g. Vander Wall 1993), but critical testing should be based on demographic data (Hanzawa et al. 1988). Testing needs to demonstrate both that seeds are dispersed disproportionately to a particular patch type and that the patch is more suitable for establishment than sites at random (Nakashizuka et al. 1995). In *A. turbinata*, changes in location of the seeds through secondary dispersal were investigated, as well as the survival and growth of seedlings at their destinations (Hoshizaki et al. 1999). Although light was most important in determining the survival and growth of seedlings, light levels at seed destinations did not differ from those at the locations of seeds before dispersal nor those on the surrounding forest floor. Therefore, this hypothesis is rejected in *A. turbinata* (Hoshizaki et al. 1999).

These three hypotheses are not mutually exclusive, so evaluating the relative importance of the hypotheses is also important for evolutionary implications for seed dispersal (Wenny 2001). Hoshizaki et al. (1999) examined the relative importance of the colonization and escape hypotheses using a statistical model, and showed that light level was a more important determinant of seedling survival than seedling density. Therefore, the colonization hypothesis is more important in this case. Herbivory did not show any density dependence, suggesting also that the significance of the escape hypothesis may be weak. Thus, the role of rodents in dispersing large seeds of *A. turbinata* is most important for finding suitable sites with more light, merely by enlarging the seed shadow.

### 7.6.2 Are rodents mutualistic dispersers?

While rodents are effective seed dispersers, they also impose heavy damage on the *A. turbinata* population through seed predation and seedling herbivory. Are they really mutualistic seed dispersers, more than antagonistic predators? First of all, the burying of seeds by rodents may be beneficial for *A. turbinata*, because the seeds are prone to desiccation (Katsuta et al. 1998); seeds may lose vigor without being hoarded underground. This effect might be subtle, considering that most of the fallen seeds were hoarded. Nonetheless it may be suggestive evidence of mutualism (Steele & Smallwood 2002).

In another view, a comparison of seedling spatial patterns may help to answer the above question. In autumn 2002, the legitimate seed dispersers (*Apodemus speciosus*) were much sparser (ca. 2 mice/ha) than usual (20-50 mice/ha). In the following spring, >80% of emerged seedlings were beneath the canopy of conspecific adults (Fig. 8); the extent of seed-shadow enlargement was much less than in 'normal' years, despite that seedlings were especially more abundant than usual (4070 vs. 100-2000 seedlings/ha). Therefore, *A. turbinata* seems not to be able to



**Fig. 8.** Contrasting spatial distributions of seedling emergence under conditions with and without effective dispersal agents. Patterns for years (a) when rodent composition and densities in the preceding autumn were at 'normal' levels and (b) when the autumn density of the legitimate seed disperser, *Apodemus speciosus*, was extremely low (see also text). Seedling densities were 1120 seedlings/ha in 2000 and 4070 in 2003. The same 0.9-ha areas in the 1-ha plot are shown with a broken frame.

enlarge the seed shadow in the absence of legitimate seed dispersers. Forest voles such as *Eothenomys andersoni* have intermediate food habits between granivores and herbivores (Shimada & Saitoh 2006), so that they also cache *A. turbinata* seeds in this forest. Although they were abundant in autumn 2002 (27 voles/ha), the seedling spatial pattern suggests their inferiority in moving seeds beyond source trees (Vander Wall 1990). Considering the strong impact of rodent herbivory (Sect. 5.1), *E. andersoni* are regarded as antagonistic predators for both seeds and seedlings. Thus regeneration of *A. turbinata* may rely on scatterhoarding by *A. speciosus*, suggesting a mutualistic relationship between them.

## 7.7 Annual variation

Regeneration of *A. turbinata* was highly variable among years. This may reflect complicated indirect interactions with rodents and a co-occurring large-seeded tree, *Fagus crenata*, that shares seed predators/dispersers with *A. turbinata*. The nature of the indirect interactions and its consequences for *A. turbinata*'s regeneration have been overviewed in previous papers (Hoshizaki & Hulme 2002; Hoshizaki & Miguchi 2005), and so only the demographic features of regeneration is briefly mentioned here.

The population produced seeds in 12 of 13 years studied (1992-2004), and its magnitude varied little among years ( $CV = 74\%$ ) (Hoshizaki et al. 1997; Hoshizaki & Hulme 2002 and unpublished data). In contrast, seedling numbers showed a greater among-year variation, ranging from 17 to 4070 seedlings/ha ( $CV = 116\%$ ). These patterns suggest that the regeneration of *A. turbinata* is rarely seed-limited. The regeneration may be determined not only by seed dispersal but also by the balance among abundances of seedfall, the legitimate seed-disperser (*A. speciosus*), and the antagonistic herbivores (*E. andersoni*). Masting of *F. crenata* causes a marked increase in rodent populations and, in turn, influences *A. turbinata* regeneration; too-high and too-low levels of rodent population under a given seed abundance may reduce regeneration success (Hoshizaki & Hulme 2002; Hoshizaki & Miguchi 2005).

## 7.8 Implications for life history in the riparian habitats

Although the regeneration was strongly limited by rodents, dispersal via rodent seed hoarding mitigates the negative impact, and seedlings are, to some extent, resistant to herbivory in *A. turbinata*. The large seed appears essential to establish a seedling bank in the understory of riparian habitats, especially under rich herbaceous vegetation. These features are particularly characteristic to *A. turbinata*, showing a remarkable contrast to other co-occurring riparian trees in which regeneration is mostly microsite-limited (Masaki et al. 2007).

Rodents may play further roles in riparian habitats. First, seeds of *A. turbinata* are often delivered to various habitats including upper slopes as well as riparian microhabitats (Hoshizaki et al. 1999). This suggests that rodents have the ability to deliver seeds across various habitats associated with the complex disturbance regime including long-distance dispersal (LDD). Second, seed burial via caching may also be effective not only in protecting from drought as mentioned above but also in preventing the seeds from being swept away with floods (Goto & Hayashida 2002). These features may support the stable population structure for *A. turbinata* in riparian forests (Kaneko et al. 1999; Suzuki et al. 2002).

The regenerative interactions reviewed here are not characteristic only of riparian forests. Nonetheless, *A. turbinata* populations are disproportionately distributed in riparian areas (Kaneko et al. 1999; Suzuki et al. 2002). Clearly, later life stages (i.e. saplings and other immature stages; Kaneko et al. 1999) seem important in *A. turbinata*, as a representative riparian species, to link the high capabilities of habitat colonization and of seedling-bank formation and the topographic bias of the population.

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